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DISTRIBUTION OF SEAGRASSES AND ASSOCIATED MACROALGAE IN SOUTH SULAWESI, INDONESIA

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SUMMARY

Eleven seagrass species were found in South Sulawesi, Indonesia. Seagrasses occurred in five different habitats, i.e. intertidal terrigenous mudflats, shallow terrigenous sandy bays, coastal reef flats, reef flats of patch reefs, and sandy reef bases, from the intertidal to a maximum depth of 35 m. *Thalassia hemprichii* and *Enhalus acoroides* were the dominant constant species of stable environments (permanently present in climax vegetations). *Cymodocea rotundata*, *Halodule uninervis* and *Halophila ovalis* were the dominant pioneering species in the area. A considerable number (117) of macroalgal taxa were found associated with seagrass vegetation, but only 13 of these were found exclusively in association with seagrasses. Macroalgal biomass in the seagrass beds was usually low (< 5 g AFDW m^{-2}). However, in stressed habitats macroalgae may contribute up to 50% to the total biomass, notably during periods of occasional blooming. Species diversity of seagrasses and associated macroalgae was much lower in stressed habitats, which are characterized by heavy sedimentation, physical instability of the substratum, or high turbidity.

INTRODUCTION

Seagrass communities are important components of tropical reefs (Van der Land, 1989; Nienhuis et al., 1989). In the present paper we use the term 'reef' in the broad sense as suggested by Van der Land (1989: 233). We also include some of the hard and soft bottom communities, which are kept separate by Nienhuis et al. (1989: 197). In reef systems, seagrasses often form an important element, occurring in sandy environments on reef flats, along beaches, and at reef bases. They also occur on tropical mudflats and other soft bottoms without coral growth. Their importance in stabilizing sediments, as feeding and nursery areas for many fish and crustacean species, and as substratum for many epiphytes, is generally recognized (Phillips, 1978; Fonseca & Fisher, 1986; Bell & Pollard, 1989; Borowitzka & Lethbridge, 1989). Seagrass beds are amongst the most productive of submerged aquatic ecosystems (Zieman & Wetzel, 1980).

In the Indonesian Archipelago, little study has been carried out on seagrass communities. During the Snellius-II Expedition (1984–1985) the seagrass communities studied (Brouns, 1985; Lindeboom & Sandee, 1989; Nienhuis et al., 1989) were each only visited for relatively short periods and observations were largely restricted

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to shallow water habitats. In long-term studies of seagrass communities in Papua New Guinea, Brouns & Heijs (1986: 405; 1992) distinguished four communities: 1) sheltered, muddy mid-eulittoral, 2) sheltered and exposed, non-muddy, mid-eulittoral, 3) lower eulittoral to upper sublittoral, and 4) lower sublittoral. They also restricted their observations mainly to the shallow habitats. They concluded that the associated macroalgae composition of seagrass communities was mainly determined by the substratum characteristics, that the number of characteristic associated macroalgae was very small, and that the contribution of associated macroalgae in the total biomass of seagrass communities was generally not higher than 5–10%, with an observed maximum of 55%.

In the present paper, results of a long term study (October 1988–February 1992) of the distribution of seagrasses and associated macroalgae in South Sulawesi, Indonesia, are presented. Differences in community structures and physical environment are discussed.

MATERIAL AND METHODS

The present study was carried out in South Sulawesi (Indonesia) between October 1988 and February 1992 in the framework of the Buginesia programme (projects III and IV), a cooperative multidisciplinary research programme in marine science between the Hasanuddin University (Ujung Pandang, Indonesia) and several Dutch universities and institutes. The study area is governed by a monsoon climate. The NW monsoon lasts from about November to April and the SE monsoon from May to October. The NW monsoon brings heavy rainfall (approximately 3000 mm annually). Maximum tidal amplitude in the area is 130 cm. Surface water temperatures vary between 26.5 and 32.5 °C.

Data on the distribution of seagrasses and associated macroalgae were collected during repeated visits to the following locations: Barang Lompo (BL), Bone Tambung (BT), Gusung (GU), Gusung Tallang (GT), Kapoposang (KP), Kudingareng Keke (KK), Kudingareng Lompo (KL), Lae Lae (LL), Langkai (LA), Lanyukang (LU), Palanro (PA), Samalona (SA), Tanjung Bira (BI) (Fig. 1).

Seagrasses and associated macroalgae were studied in five different habitat types: 1) intertidal terrigenous mudflats, 2) shallow terrigenous sandy bays, 3) coastal reef flats, 4) reef flats of patch reefs, and 5) sandy reef bases (> 10 m depth).

Intertidal terrigenous mudflats (e.g. Gusung Tallang, Takalar, Tana Keke, and parts of Teluk Laikang), deposited by rivers, are characterized by soft muddy sediments originating from the mainland. The water at these sites is usually very turbid.

Shallow terrigenous sandy bays (e.g. Palanro, Barru, parts of Teluk Laikang) are dominated by terrigenous sands and limited river input, resulting in low turbidity.

Coastal reef flats (e.g. Tanjung Bira, Selayar) are dominated by sandy carbonate sediments, and clear water. These reef flats range from the intertidal zone down to depths of approximately 5 m.

Reef flats of patch reefs (e.g. Barang Lompo, Bone Tambung, Barang Caddi, Kudingareng Lompo, Samalona, Kudingareng Keke, Langkai, Lanyukang, Kapoposang) have sandy carbonate sediments and clear water. This habitat is comparable to that of coastal reef flats, but most patch reefs appear to be more susceptible to wave

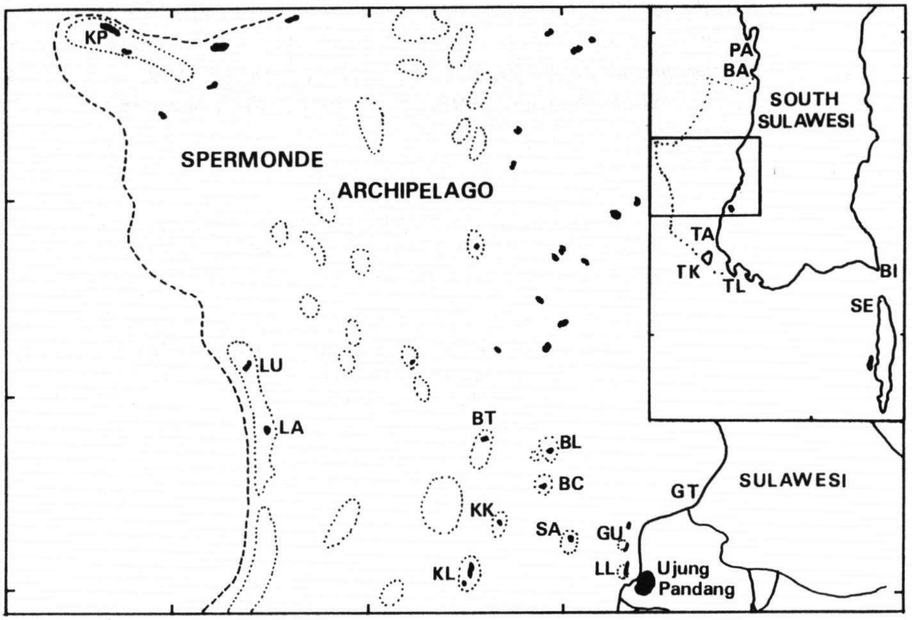


Fig. 1. Map of the study area, showing the locations mentioned in the text. Abbreviations: BA = Barru; BC = Barang Caddi; BI = Tanjung Bira; BL = Barang Lompo; BT = Bone Tambung; GT = Gusung Tallang; GU = Gusung; KK = Kudingareng Keke; KL = Kudingareng Lompo; KP = Kapoposang; LA = Langkai; LL = Lae Lae; LU = Lanyukang; PA = Palanro; SA = Samalona; SE = Selayar; TA = Takalar; TK = Tana Keke; TL = Teluk Laikang.

activities and experience more physical instability of the substratum. Most of these reef flats range from the intertidal to c. 2 m water depth, but the reef flats of some islands (e.g. Kapoposang, Langkai) have parts which reach down to more than 5 m water depth.

The sandy reef base, below which coral growth is largely absent, is characterized by considerable sedimentation. At most of the islands in the study area, reef base sediments start accumulating at depths around 10 to 15 m, but at some nearshore islands (e.g. Gusung, Lae Lae) coral growth stops at a depth of approximately 5 m. Although usually overlain by a water column of low turbidity characteristic of reef environments, the reef base normally receives less than 25% of the irradiance (PAR) measured just below the water surface (Erftemeijer, in press).

Some additional data on seagrass distribution were collected at Barang Caddi (BC), Barru (BA), Takalar (TA), Tana Keke (TK), Teluk Laikang (TL), and Selayar (SE), but macroalgae were not studied at these localities. Representative specimens of most algae and seagrass taxa were collected and stored in a wet collection or a herbarium collection. All collections are deposited in the Rijksherbarium, Leiden, The Netherlands. Duplicates were sent to Herbarium Bogoriense, Bogor, Indonesia. For each locality, short descriptions were made of the habitat, including sediment type, turbidity and water depth. Some approximate data were collected on the biomass of the seagrasses and macroalgae. Quantitative data on the total distribution and coverage of macroalgae and on physical and biological parameters in seagrass beds in the study area are presented elsewhere (Verheij, 1993a, b; Verheij & Prud'homme van Reine, 1993; Erftemeijer, in press).

Table 1. Occurrence of seagrass species in different habitat types in South Sulawesi, Indonesia, with details on the range of water depths in which they were found (*** = well developed in this habitat, widespread occurrence; * = poorly developed, only a few observations, very limited in cover/biomass).

Macroalga	Depth range (m)	Intertidal terrigenous mudflats	Shallow terrigenous sandy bays	Coastal reef	Reef flats of patch reefs	Sandy reef base
Hydrocharitaceae						
Enhalus acoroides	0–5	***	***	***	***	
Halophila decipiens	5–35					***
Halophila ovata	0–2		*		*	
Halophila ovalis	0–30	*	***	***	***	***
Thalassia hemprichii	0–5	*	***	***	***	
Potamogetonaceae						
Cymodocea rotundata	0–5	*	***	***	***	
Cymodocea serrulata	0–3 (20)		***		*	*
Halodule uninervis	0–20	*	***	***	***	*
Halodule pinifolia	0–2	***	***	***	***	
Syringodium isoetifolium	0–3		***	***	***	
Thalassodendron ciliatum	0–3			***		

Table 2. Overview of phenological data (flowering and fruiting) of six seagrass species collected in the study area between October 1988 and February 1992. No observations of flowers, fruits or seeds were made for *Halophila ovata*, *Cymodocea serrulata*, *Halodule uninervis*, *Halodule pinifolia*, and *Thalassodendron ciliatum*.

month:	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Hydrocharitaceae												
Enhalus acoroides	*	*	*	*	*	*	*	*	*	*	*	*
Halophila ovalis								*	*		*	*
Halophila decipiens								*	*	*	*	
Thalassia hemprichii		*	*	*	*			*	*	*	*	*
Potamogetonaceae												
Cymodocea rotundata											*	
Syringodium isoetifolium								*	*	*	*	*

RESULTS

The seagrass species

We identified eleven seagrass species which were distributed over a wide range of habitats and depths in the study area (Table 1). Descriptions and illustrations of these species are to be found in den Hartog (1970), Brouns & Heijs (1986) and Phillips & Meñez (1988). Common names, as used by Fortes (1990), are not incorporated. The following overview provides details on morphological variability, substratum, depth and phenology of the seagrass species in the study area. Data on phenology are summarized in Table 2.

Family HYDROCHARITACEAE

Enhalus Rich.

Enhalus acoroides (Linn. f.) Royle, 1840: 453.

Enhalus acoroides occurred in a wide range of habitats (Table 1), with substrata varying from soft terrigenous mud to coarse carbonate sediments on coral reef flats. The species was not found deeper than 5 m and occurred in both monospecific and mixed seagrass stands. The species showed considerable morphological variations within the studied area, with the average length and width of leaves generally being greatest in high nutrient environments (Erftemeijer, in press). A maximum leaf length of over 2 m and a maximum leaf width of 18 mm were recorded from an intertidal mudflat near the coast of the mainland (Gusung Tallang; 1990). Apices of tall leaves were usually eroded due to wave energy and occasional exposure at low tides. Roots at Gusung Tallang were up to 30 cm long and penetrated deep into the sediment. The species had flowers and fruits during all months of the year.

Halophila Du Petit Thouars

Remarks: Identification of *Halophila* species was based on the pattern and number of cross-veins, following Meñez et al. (1983): Leaves with 4–7 pairs of cross-veins [= *H. ovata* (as *H. minor* in Meñez et al.)]; leaves with more than 12 pairs of cross-veins (= *H. ovalis*). *Halophila decipiens* always had distinct lateral veins (which were absent in the other species), with cross-veins present but less conspicuous. No material was found with 8–11 pairs of cross-veins.

Halophila decipiens Ostenfeld, 1902: 260.

Halophila decipiens was only encountered in deep-water reef base sediments (six localities) at depths between 5 and 35 m (Table 1). It formed monospecific meadows or occurred in mixed beds with *H. ovalis*. In contrast with the other *Halophila* species this species is monoecious, with male and female flowers developing on the same plant (Den Hartog, 1970). Leaf size was in accordance to literature (10–25 mm long; 3–6 mm wide). Flowering and/or fruiting were encountered from August to November.

Halophila ovalis (R. Brown) Hooker f., 1858: 45.

Halophila ovalis occurred in all habitats examined (Table 1) and at all depths investigated, from the upper intertidal zone down to 30 m. It is known to have a very wide ecological tolerance and is generally considered a pioneer species. Although usually present in mixed seagrass beds, the species can also form extensive monospecific beds on unstable reef flats (e.g. Kudingareng Keke) and usually dominates meadows on sandy bottoms of reef slopes characterized by heavy sedimentation. It is known to tolerate coverage by sand or mud and has been repeatedly found completely covered by sediments but still in good condition (Den Hartog, 1970). The species showed a large morphological variation in the study area, with leaves usually largest in high nutrient environments, where their leaf blades grew up to 3.2 cm long and 1.3 cm wide. Small plants were sometimes difficult to be distinguished from *Halophila ovata*. Flowers and/or fruits were encountered from August to December and only occurred in deeper water (10–30 m).

Halophila ovata Gaudichaud, 1827.

Halophila ovata was found in sheltered localities on sandy bottoms in the lower part of the eulittoral and the uppermost part of the sublittoral to 2 m depth (Table 1). Leaf size was in accordance to Den Hartog (1970) (7–14 mm long; 3–5 mm wide). Flowers and fruits were not found; Den Hartog (1970) reported flowering and fruiting from January to July.

Thalassia Banks ex König

Thalassia hemprichii (Ehrenberg) Ascherson, 1871b: 242.

Thalassia hemprichii was common on shallow reef sediments and terrigenous sandy bays (Table 1). It was, however, practically absent from terrigenous mudflats; only a few shoots were retrieved at Gusung Tallang. The species was not found at depths greater than 5 m. Leaves showed a relatively large variation in size throughout the study area, with a maximum length of 30.5 cm and a maximum width of 14 mm. Leaf size was generally larger in high nutrient environments (Erftemeijer, in press). However, several large-sized plants were encountered among small-sized plants on the reef flat of Langkai, an offshore reef island. Indications of generative reproduction were encountered during 9 different months of the year, which suggests that the species flowers and fruits throughout the year.

Family POTAMOGETONACEAE

Cymodocea König

Cymodocea rotundata Ehrenberg & Hemprich ex Ascherson, 1871a: 84.

Cymodocea rotundata was found in shallow-water habitats (up to 5 m water depth, but mainly confined to the upper 2 m) on both carbonate and terrigenous sediments ranging from coarse sand to sandy mud (Table 1). Leaf morphology showed some variation, with a maximum length of 31 cm and a maximum width of 4 mm recorded from coastal terrigenous sediments. It is a dominant pioneering species along beach-side fringes of dense seagrass beds and along blow-outs. No flowering was observed in the study area, but seeds were encountered in November at Langkai island (reef flat). Den Hartog (1970) reported occasional observations of flowering and fruiting in April, June and November.

Cymodocea serrulata (R. Brown) Ascherson & Magnus in Ascherson, 1871a: 84.
Cymodocea serrulata was encountered at five localities (BA, KP, LA, PA, TL). It occurred on terrigenous and carbonate sands of a relatively coarse composition, usually in shallow water (to 3 m depth), but one small patch of the species was encountered at 20 m depth at Langkai (July 3, 1990) (Table 1). Leaf morphology was in accordance with literature (6–15 cm long; 2–4 mm wide). Generative reproduction was not observed in the study area, and flowers and fruits have been only occasionally reported from elsewhere (January, April, October, November; Den Hartog, 1970).

Halodule Endlicher

Halodule pinifolia (Miki) Den Hartog, 1964: 309.
Halodule pinifolia occurred on various intertidal substrata, ranging from soft terrigenous mud (Takalar) to coarse carbonate sand (Table 1). The species was never found in mixed vegetations among other species. It usually occurred in shallow water (< 1 m) as a pioneer in a narrow strip along the beach, where other species were absent, or in places where the vegetation had been destroyed by mechanical disturbance (e.g. anchoring places for small boats at the reef islands). On terrigenous muddy substratum, however, it sometimes formed relatively dense monospecific meadows. Leaf lengths and widths were within the range reported by Phillips & Meñez (1988) with a maximum length of 12 cm and a maximum width of 1.5 mm. The species was distinguished from the narrow-leaved form of *Halodule uninervis* by the absence of nerves and the external appearance of leaf tips (Meñez et al., 1983): leaves of *H. uninervis* had tips with each two acuminate teeth and a distinct median nerve, whereas in the leaves of *H. pinifolia* the tips had a furcate midrib and irregular teeth and the leaves had no nerves at all. Flowers and fruits were not observed, but flowering of this species in October and November has been reported from Queensland, Australia (Den Hartog, 1970).

Halodule uninervis (Forsskål) Ascherson in Boissier, 1882: 24.
Halodule uninervis occurred in all habitats investigated at 0–20 m depth on substrata ranging from coarse carbonate sand to soft terrigenous mud (Table 1). It was dominant in the upper intertidal zone but also occurred among other species in dense mixed beds in shallow water. It was also encountered at greater depths (down to 20 m, Bone Tambung) growing on coarse reef base sediments in meadows dominated by *Halophila ovalis* or *Halophila decipiens*, but there it did not develop into large stands. Two growth forms were distinguishable: a narrow-leaved form (leaf-width < 1 mm) and a broad-leaved form (leaf width 1.5 to 3 mm). Although Den Hartog (1970) considered these as environmental modifications of the same species, we sometimes found both growth forms mixed at the same locality (e.g. Bone Tambung reef flat),

Table 3. Occurrence of macroalgal taxa in different seagrass habitat types in South Sulawesi, Indonesia, with details on the range of water depths in which they were found (*** = well developed in this habitat, widespread occurrence; * = poorly developed, only a few observations, very limited in cover/biomass).

Macroalga	Depth range (m)	Intertidal terrigenous mudflats	Shallow terrigenous sandy bays	Coastal reef	Reef flats of patch reefs	Sandy reef bases
CHLOROPHYTA						
Acetabularia dentata Solms-Laubach	1–5			*	*	
Anadyomene stellata (Wulfen) C. Agardh	1–2				*	
Avrainvillea amadelpha (Montagne) A. Gepp et E.S. Gepp	1–2				*	
A. obscura (C. Agardh) J. Agardh	1–5			***	***	
Boergesenii forbesii (Harvey) J. Feldmann	1–5			*	*	
Boodlea composita (Harvey) Brand	1–2			***	***	
Caulerpa brachypus Harvey	1–35			*		***
C. cupressoides (Vahl) C. Agardh	1–20			*	*	*
C. buginense Verheij et Prud'homme van Reine	15					*
C. elongata Weber-van Bosse	1–5			*	*	
C. lentillifera J. Agardh	1–20	***		*		
C. lessonii Bory de Saint-Vincent	15–25					*
C. racemosa (Forsskål) J. Agardh	1–30					
ecad *corynephora*	1–5	***				
ecad *macrodisca*	15–30					***
ecad *occidentalis*	1–5			*	*	
ecad *peltata*	1–10			*	*	
ecad *racemosa*	1–5			*	*	
C. serrulata (Forsskål) J. Agardh	1–15		*	*	*	*
C. sertularioides (S.G. Gmelin) Howe	1–15			*	*	*
C. taxifolia (Vahl) C. Agardh	1–30			*		*
Chaetomorpha crassa (C. Agardh) Kützing	10–30				*	***
Chlorodesmis fastigiata (C. Agardh) Ducker	1–5			*	*	
C. hildebrandtii A. Gepp et E.S. Gepp	1–5			*	*	
Codium arabicum Kützing	1–3				*	
C. bartlettii Tseng et Gilbert	15–20					***

C. edule P.C. Silva	1–5				*	
C. geppiorum O.C. Schmidt	10–30					***
Dictyosphaeria cavernosa (Forsskål) Børgesen	1–5			*	*	
D. versluysii Weber-van Bosse	1–5				*	
Enteromorpha clathrata (Roth) Greville	1–5	***		***	***	
E. compressa (Linnaeus) Nees	1–5				***	
Halimeda copiosa Goreau et Graham	15–20					*
H. cylindracea Decaisne	1–20			***	***	*
H. discoidea Decaisne	1–20			*	*	*
H. gigas W.R. Taylor	1–15			*	*	*
H. macroloba Decaisne	1–15	***		***	***	*
H. macrophysa Askenasy	1–5				*	
H. micronesica Yamada	1–5				*	
H. opuntia (Linn.) Lamouroux f. *opuntia*	1–15		***	***	***	
H. simulans Howe	1–20			*	*	*
H. taenicola W.R. Taylor	10–25					*
Neomeris annulata Dickie	1–5	*		*	*	
N. vanbosseae Howe	1–5	*		*	*	
Udotea argentea Zanardini	1–20			***	***	*
U. flabellum (Ellis et Solander) Howe	1–15	***			***	*
U. glaucescens Harvey ex J. Agardh	15–20					*
Ulva reticulata Forsskål	1–5	***				
Valonia aegagrophila C. Agardh	1–5			*	*	
V. fastigiata Harvey ex J. Agardh	1–5			*	*	
PHAEOPHYTA						
Chnoospora implexa (Hering) J. Agardh	1–5				*	
Dictyota bartayresiana Lamouroux	1–5			*	*	
D. ciliolata Kützing	1–5				*	
D. crenulata J. Agardh	1–15				*	*
D. dichotoma(Hudson) Lamouroux	1–5				*	
D. linearis (C. Agardh) Greville	1–5		***		***	
D. cf. *rugulosa* Lucas	1–5			*	*	
Hydroclathrus clathratus (C. Agardh) Howe	1–15			***	***	*
H. tenuis Tseng et Lu	1–5				*	

(Table 3 continued)

Macroalga	Depth range (m)	Intertidal terrigenous mudflats	Shallow terrigenous sandy bays	Coastal reef	Reef flats of patch reefs	Sandy reef bases
(Phaeophyta continued)						
Padina australis Hauck	1–10			***	***	
P. minor Yamada	1–5			*	*	
P. sanctae-crucis Børgesen	1–5				*	
P. tenuis Bory de Saint-Vincent	1–5			*	*	
Sargassum hemiphyllum (Turner) C. Agardh	1–2				*	
Stypopodium flabelliforme Weber-van Bosse	20					***
Turbinaria decurrens Bory de Saint-Vincent	1–2				***	
T. ornata (Turner) J. Agardh	1–2			*	***	
RHODOPHYTA						
Acantophora muscoides (Linnaeus) Bory de Saint-Vincent	1–2			***	***	
A. spicifera (Vahl) Børgesen	1–2			***	***	
Actinotrichia fragilis (Forsskål) Børgesen	1–2				*	
Amphiroa fragilissima (Linnaeus) Lamouroux	1–10		***	***	***	
Ceramium spec.	1–5			*	*	
Ceratodictyon intricatum (C. Agardh) R.E. Norris	1–5			*	*	
C. spongiosum Zanardini	1–5			***	***	
Champia parvula (C. Agardh) Harvey	1–15			*	*	*
Eucheuma denticulatum (N.L. Burman) Collins et Hervey	1–2	*			*	
Fosliella spec.	1–5			*	*	
Galaxaura oblongata (Ellis et Solander) Lamouroux	1–5			***	***	
G. obtusata (Ellis et Solander) Lamouroux	15–20					*
G. subverticillata Kjellman	1–5			***	***	
Gelidiella acerosa (Forsskål) Feldmann et Hamel	1–5			***	***	
Gelidium pusillum (Stackhouse) Le Jolis	1–5			*	*	
Gelidium spec.	1–10			*	*	
Gracilaria arcuata Zanardini	1–5			*	*	
G. blodgettii Harvey	1–5	***				

G. coronopifolia J. Agardh	1–5				*	
G. eucheumoides Harvey	1–2			*	*	
G. salicornia (C. Agardh) Dawson	1–2	***		***	***	
G. verrucosa (Hudson) Papenfuss	1–2	***			*	
Halymenia acuminata (Holmes) Okamura	1–5				*	
H. durvillaei Bory de Saint-Vincent	1–2			*	***	
Hydrolithon reinboldii (Weber-van Bosse et Foslie) Weber-van Bosse	1–20			***	***	***
Hydrolithon spec.	1–10				*	
Hypnea pannosa J. Agardh	1–5			*	***	
Hypnea spec.	1–5				*	
Kallymenia feldmannii Codomier	15–20					*
Kappaphycus alvarezii (Doty) Doty	1–2	*		***	***	
K. striatum (Schmitz) Doty	1–2	* (?)			*	
Laurencia mariannensis Yamada	1–2				*	
L. papillosa (C. Agardh) Greville	1–5			***	***	
L. parvipapillata Tseng	1–2				*	
Leveillea jungermannioides (Hering et Martens) Harvey	1–30			*	*	*
Liagora ceranoides Lamouroux	1–5				***	
Lithophyllum tamiense Heydrich	1–5			*	*	
Lithophyllum spec.	1–10				*	
Mastophora rosea (C. Agardh) Setchell	1–3			***	*	
Mesophyllum erubescens (Foslie) Lemoine	1–30			*	*	***
M. syrphetodes Adey, Townsend et Boykins	15–45					***
Neogoniolithon brassica-floridum (Harvey) Setchell & Mason	1–5					
ecad *fosliei*	1–5			***	***	
ecad *frutescens*	1–5			***	***	
Portieria hornemannia (Lyngbye) P.C. Silva	1–5			***	***	
Pterocladia caloglossoides (Howe) Dawson	1–15				*	*
P. caerulescens (Kützing) Santalices	1–5				*	
Sporolithon ptychoides Heydrich	1–15				***	***
Spyridia filamentosa (Wulfen) Harvey	1–5	***		***	***	
Trichogloea requierii (Montagne) Kützing	1–5			*	*	
Zellera tawallina Martens	10–20					*

which might indicate two different forms rather than ecotypes. We recorded a maximum leaf length of 17.4 cm (broad-leaved form). Flowers and fruits were not encountered but are reported to occur in October and November (Den Hartog, 1970).

Syringodium Kützing

Syringodium isoetifolium (Ascherson) Dandy in Dandy & Tandy, 1939: 116.

Syringodium isoetifolium was found at seven localities (BA, BI, BL, BT, KP, LA, PA), all on sandy substratum (on reef flats and at a terrigenous sandy bay) to a maximum depth of 3 m (Table 1). We recorded a maximum leaf length of 23 cm and a maximum width of 2 mm. The species did not occur in places which experience long-lasting exposure during low water of spring tides. *Syringodium isoetifolium* did not form monospecific stands, but always occurred in stands dominated by other species. Flowers were found from August to December. Massive flowering was encountered at Langkai in November 1989 and September 1990. Fruits were not observed.

Thalassodendron Den Hartog

Thalassodendron ciliatum (Forsskål) Den Hartog, 1970: 188.

Thalassodendron ciliatum was only found at Tanjung Bira, a small peninsula in the southeastern corner of South Sulawesi. Here, the species occurred from the lower intertidal down to depths of approximately 3 m. *Thalassodendron ciliatum* appears to favour coral rubble substrata, where dense stands were found, but also occurs in mixed vegetations (e.g. with *Thalassia hemprichii*, *Syringodium isoetifolium* and *Enhalus acoroides*) on finer carbonate sediments. Brouns (1985) also reported the species from Selayar (South Sulawesi), where it had a rhizome layer of up to 70 cm in thickness. *Thalassodendron ciliatum* has a disjunct distribution pattern, being common in the Red Sea and western Indian Ocean, down along the east coast of Africa (Madagascar, Seychelles, Comores, Mascarenes, Maldives, Chagos Archipelago), but also occurring in the eastern part of Indonesia, the Philippines, the Solomon Islands, the Xisha Archipelago, Papua New Guinea and Australia (Den Hartog, 1970, and pers. comm.). Tanjung Bira (South Sulawesi) apparently is the westernmost known locality of its eastern distribution areal. It remains unclear why the species does not occur at any of the localities along the west coast of South Sulawesi. Leaf morphology was in accordance to Den Hartog (1970) (10–15 cm long; 6–13 mm wide). The species was often densely covered with epiphytic algae (mainly coralline algae), notably on its stems. Flowering or fruiting was not observed in the study area.

The associated macroalgae

During the present study, 117 taxa of macroalgae (50 Chlorophyta, 17 Phaeophyta, and 50 Rhodophyta) were found associated with seagrass beds in the five different habitats (Table 3). Of these, only 13 taxa were found exclusively in association with seagrass vegetation within the study area: *Avrainvillea stellata, Caulerpa*

Table 4. A compilation of macroalgal epiphytes observed on the seagrasses, with their position on the plants.

Macroalga	leaves	stems	Macroalga	leaves	stems
Boodlea composita	*	*	*Actinotrichia fragilis*	*	*
Chaetomorpha crassa	*		*Fosliella* spec.	*	
Enteromorpha clathrata	*	*	*Gelidium pusillum*	*	
Enteromorpha compressa	*	*	*Gelidium* spec.	*	
			Hypnea pannosa	*	
			Hypnea spec.	*	
Dictyota ciliolata	*	*	*Leveillea jungermannioides*	*	*
Dictyota dichotoma	*		*Mastophora rosea*	*	*
Dictyota linearis	*	*	*Spyridia filamentosa*	*	
Hydroclathrus clathratus	*		*Trichogloea requierii*	*	*

buginense, Caulerpa racemosa ecad *corynephora, Chaetomorpha crassa, Dictyota ciliolata, Dictyota linearis, Hydroclathrus tenuis, Actinotrichia fragilis, Gracilaria salicornia, Trichogloea requierii, Fosliella* spec., *Mastophora rosea,* and *Neogoniolithon brassica-floridum* ecad *frutescens.* The remaining 104 taxa also occur in reef communities without seagrass vegetation (Verheij & Prud'homme van Reine, 1993).

Most taxa were found growing attached to the substratum between the seagrass plants, although some were free-living (e.g. *Ulva reticulata, Hydrolithon reinboldii,* and *Neogoniolithon brassica-floridum* ecad *frutescens*). Eighteen taxa occurred as epiphytes on seagrass leaves and/or stems (Table 4).

The habitats

Intertidal terrigenous mudflats only harboured monospecific seagrass beds. Dominant species were *Enhalus acoroides* and *Halodule pinifolia,* but a few specimens of *Thalassia hemprichii, Halophila ovalis* and *Cymodocea rotundata* were also collected. Macroalgae most abundant in these meadows were *Caulerpa racemosa* ecad *corynephora, Udotea flabellum, Ulva reticulata, Gracilaria salicornia,* and *G. verrucosa.*

In shallow terrigenous sandy bays, well-developed mixed-species seagrass meadows occurred which harboured up to nine different seagrass species. Associated macroalgae most abundant in this habitat were *Halimeda opuntia* forma *opuntia, Dictyota linearis,* and *Amphiroa fragilissima.*

Coastal reef flats harboured rich and dense mixed-species vegetations with up to eight species. Macroalgae most abundant in this habitat include *Avrainvillea obscura, Enteromorpha clathrata, Hydroclathrus clathratus,* and *Hydrolithon reinboldii.*

Reef flats of patch reefs usually harboured dense mixed-species seagrass meadows with up to eight seagrass species. The occurrence of nearly monospecific meadows of *Halophila ovalis* on some of the reef flats (e.g. Samalona, Kudingareng Keke) is attributed to a relatively high degree of physical instability. Macroalgae most abundant in these reef flat meadows include *Enteromorpha compressa, Udotea flabellum, Turbinaria decurrens, Halymenia durvillaei,* and *Sporolithon ptychoides.*

At the sandy reef bases of Barang Lompo, Bone Tambung, Kapoposang, Kudingareng Lompo, Kudingareng Keke, Langkai and Samalona, below which coral growth is largely absent, considerable areas were covered by pioneer seagrass species (mainly *Halophila* spp.). Other species encountered in this habitat (though sporadically and in low densities) included *Halodule uninervis* and *Cymodocea serrulata*. Macroalgae most abundant in these pioneering vegetations were *Caulerpa brachypus*, *Codium bartlettii*, *C. geppiorum*[3], *Stypopodium flabelliforme*, and *Mesophyllum erubescens*.

DISCUSSION

Eleven species of seagrass belonging to seven genera and two families were recorded in the study area. The area provides a wide range of habitats for seagrass growth. Terrigenous sediments deposited by rivers primarily occur along the west coast of South Sulawesi. Carbonate sediments of varying grain-size distribution dominate the reef flats and reef base of the islands of the Spermonde Archipelago. Coastal reef flats are dominant along the southern coastline and at Tanjung Bira in the southeast. The tropical environmental conditions permit seagrass growth all year round, with seasonal dynamics, if present, probably only related to seasonal fluctuations in rainfall. The occurrence of mixed vegetation with up to nine different seagrass species, several of which may dominate alternatively, is in contrast with the seagrass communities of the tropical Caribbean, where monospecific vegetations dominate (Zieman, 1987).

Enhalus acoroides and *Thalassia hemprichii* are by far the most dominant species in the whole area, having the widest distribution and largest biomass (Erftemeijer, in press). They are constant species, permanently present in the climax vegetation. However, in the eastern part of the study area (Tanjung Bira) *Thalassodendron ciliatum* is also one of the most abundant species. *Halophila ovalis*, *Halodule uninervis* and *Cymodocea rotundata* are the dominant pioneering species in the study area, but their overall biomass is relatively low in comparison to *Enhalus* and *Thalassia*. There was a high degree of patchiness in the seagrass beds, with several bare sand patches on reef flats contributing to the overall habitat diversity, sustaining mixed vegetations and the occurrence of pioneer species.

Phenology data on seagrasses in the study area indicate differences in the timing of floral induction between species. *Enhalus acoroides* and *Thalassia hemprichii* were found flowering and/or fruiting during most months of the year. Spring low tide exposure is known to be involved in floral induction in these species (Pettitt, 1984). Flowering in *Halophila ovalis* was only encountered in deeper water (10–25 m), although the species also occurred in shallow waters. *Halophila ovalis*, *H. decipiens*, *Cymodocea rotundata* and *Syringodium isoetifolium* were only flowering and/or fruiting between August and December. This might indicate a seasonal pattern in their reproductive behaviour. No reproductive behaviour was observed for *Halophila*

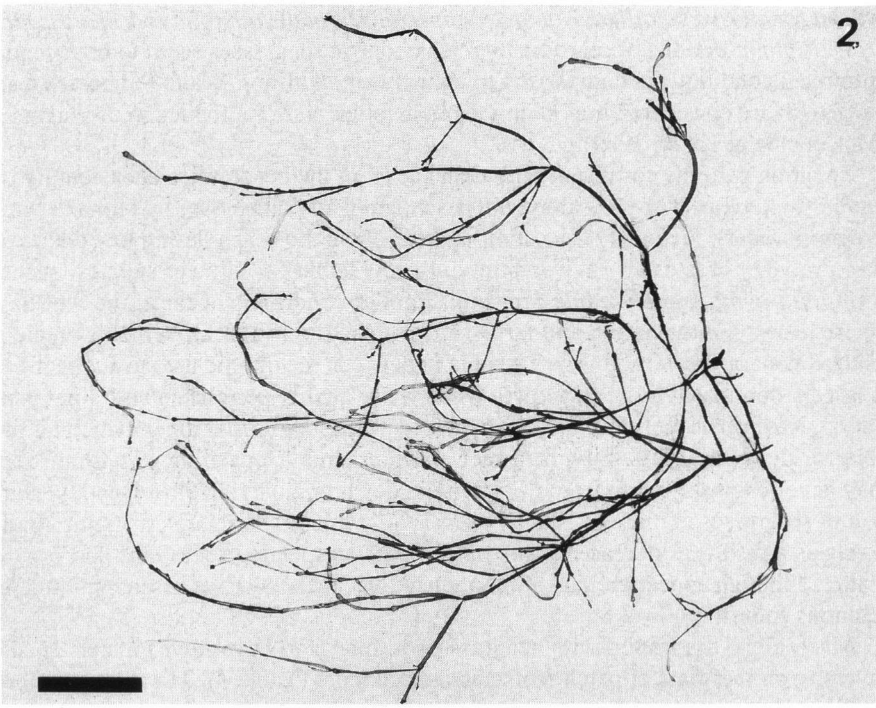
[3] Verheij & Prud'homme van Reine (1993: 400) referred to this species as *Codium geppii* O.C. Schmidt, 1923. According to the International Code for Botanical Nomenclature (1988: Art. 73.20, Rec. 73C.1, Ex. 19) the correct orthography of the epithet should be *geppiorum*.

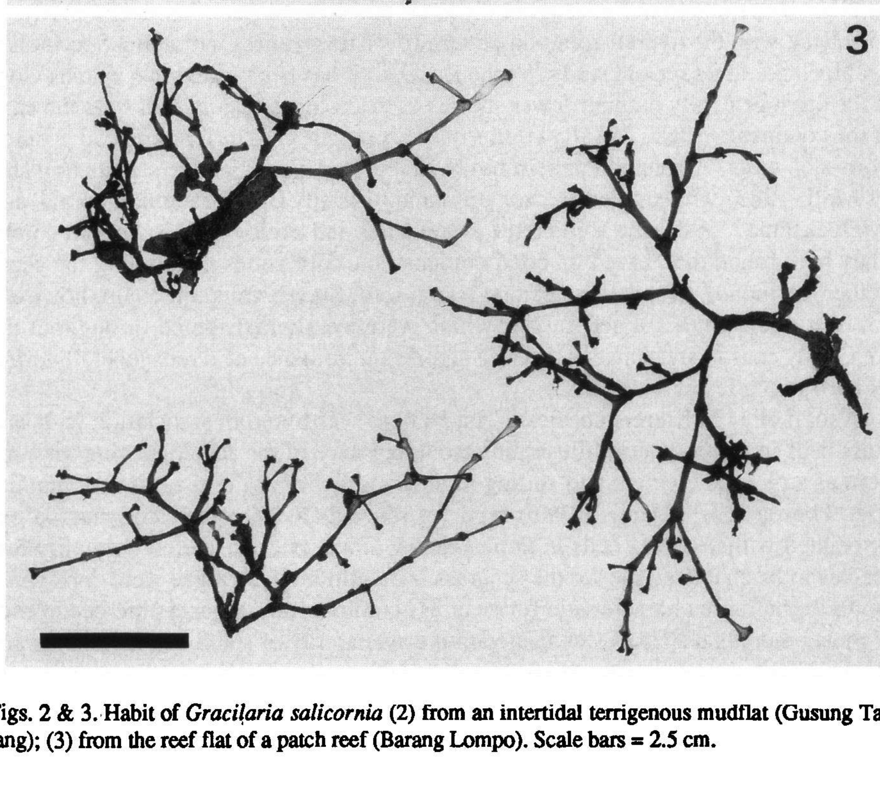
ovata, *Cymodocea serrulata*, *Halodule uninervis*, *Halodule pinifolia* and *Thalassodendron ciliatum*. Periods of reproductive behaviour in seagrasses seem to be extended in tropical conditions in comparison to temperate conditions. Water temperature and day length are considered important factors involved in floral induction of seagrasses (McConchie & Knox, 1989).

Zonation patterns correlated with distance from the beach were occasionally observed (with pioneer species along the beach, gradually taken over by climax species in deeper water). Frequent desiccation of areas along the beach during low tide exposure probably creates an environment only accessible for pioneer species, such as *Halophila ovata* and *Halodule pinifolia*. Similar conditions occur at the reef base, where heavy sedimentation and large shifts of sand by water movements create an environment of great instability. The area in between the intertidal zone and reef base is largely dominated by coral growth when water quality permits enough light penetration, leaving the reef flats at patch reefs and at coastal reefs as the only habitat suitable for dense seagrass growth in reef environments. Coastal areas without reefs may have seagrass growth from the intertidal down to greater depths. Depth penetration of seagrasses in these coastal areas is usually limited by relatively high turbidity levels as a result of increased loads of nutrients, suspended sediments and organic matter, and high concentrations of phytoplankton caused by river discharges and terrigenous runoff.

Macroalgae associated with seagrass beds appear to have their greatest species diversity on reef flats of patch reefs and coastal reefs (Table 3). The relatively large number of species found in seagrass beds on reef flats of patch reefs can partly be correlated with the overall zonation pattern (over four zones) within the Spermonde Archipelago. In a separate study (Verheij, 1993a) it has been stated that islands close to the coast generally harbour fewer species of macroalgae than islands near the edge of the continental shelf. The algal floras of the zones are also different in composition from each other. A zonation pattern has been reported earlier for the same study area by Moll (1983) who studied the zonation and diversity of scleractinian corals, and by Hoeksema (1990) who studied the systematics and ecology of mushroom corals. They both found that, based on coral composition, four zones parallelling the shore in the Spermonde Archipelago can be recognized. Such a zonation could, however, not be demonstrated for seagrasses, which were evenly distributed throughout the area. Only coastal areas that experience significant influence of rivers generally differ by harbouring fewer species.

A total of 117 different species of macroalgae was found in association with seagrass beds in the study area, illustrating the importance of the accompanying seaweed flora as structural element and adding to the complexity of the seagrass community (Den Hartog, 1979). Heijs (1985) reported more than 100 species of macroalgae associated with seagrass beds in Papua New Guinea, but considered only very few species to be characteristic for the seagrass beds. Rhizophytic algae were considered by her to be more characteristic for seagrass communities, whereas the occurrence of most other algal species was related to the availability of stabilized hard substrata. Coppejans et al. (1992) reported 31 species of macroalgae to be associated with seagrass meadows in Gazi Bay (Kenya) which were distributed according to a general pattern of zonation and succession from the mangal to deep waters.





Figs. 2 & 3. Habit of *Gracilaria salicornia* (2) from an intertidal terrigenous mudflat (Gusung Tallang); (3) from the reef flat of a patch reef (Barang Lompo). Scale bars = 2.5 cm.

Table 5. Overview of the seasonal occurrence of dominant macroalgae associated with seagrass beds. (---- = less than 0.5% coverage, ==== more than 0.5% coverage).

Macroalga	J	F	M	A	M	J	J	A	S	O	N	D
A. obscura			-	-	=	=	=	=	=	=	-	-
B. composita					-	=	=	=	=	=		
C. brachypus					-	=	=	=	=	-	-	-
C. lentillifera		-	-	=	=	=	=	=	-			
C. racemosa												
ecad *corynephora*				-	-	=	=	=	=	-	-	
ecad *macrodisca*					-	=	=	=	=	-	-	
C. crassa						-	=	=	-	-		
C. bartlettii					-	-	=	=	-	-		
C. geppiorum					-	-	=	=	=	-	-	
E. clathrata			-	-	-	=	=	=	=	-	-	
E. compressa			-	-	-	=	=	=	=	-	-	
H. cylindracea	-	-	-	-	=	=	=	=	=	-	-	-
H. macroloba	-	-	-	=	=	=	=	=	=	=	-	-
H. opuntia	-	-	=	=	=	=	=	=	=	=	-	-
U. argentea	-	-	-	=	=	=	=	=	=	=	-	-
U. flabellum		-	-	-	=	=	=	=	=	=	-	
U. reticulata						-	=	=	-	-		
D. limearis				-	-	=	=	=	=	-	-	
H. clathratus				-	-	=	=	=	=	=	-	-
P. australis				-	-	=	=	=	=	=	-	-
S. flabelliformis	-	-	-	=	=	=	=	=	=	=	=	=
T. decurrens				-	=	=	=	=	=	=	-	-
T. ornata					-	=	=	=	=	=	=	-
A. muscoides	-	-	-	-	=	=	=	=	=	=	-	-
A. spicifera	-	-	-	-	=	=	=	=	=	=	-	-
A. fragilissima	-	-	-	-	-	=	=	=	=	=	=	-
C. spongiosum	=	=	=	=	=	=	=	=	=	=	=	=
G. oblongata	-	-	-	=	=	=	=	=	=	=	=	=
G. subverticillata	-	-	-	=	=	=	=	=	=	=	=	-
G. blodgettii					-	-	=	=	=	=	-	-
G. salicornia			-	=	=	=	=	=	=	=	-	
G. verrucosa					-	-	=	=	=	-	-	-
H. durvillea					-	=	=	=	=	-	-	
H. reinboldii	=	=	=	=	=	=	=	=	=	=	=	=
H. pannosa	-	-	-	-	=	=	=	=	=	=	=	-
K. alvarezii		-	-	=	=	=	=	=	=	=	-	
L. papillosa				-	-	=	=	=	=	=	-	-
L. ceranoides				-	-	=	=	=	=	=	-	-
M. rosea	-	-	-	-	=	=	=	=	=	=	=	-
M. erubescens	=	=	=	=	=	=	=	=	=	=	=	=
M. syrphetodes	=	=	=	=	=	=	=	=	=	=	=	=
N. brassica-floridum												
ecad *fosliei*	=	=	=	=	=	=	=	=	=	=	=	=
ecad *frutescens*	=	=	=	=	=	=	=	=	=	=	=	=
P. hornemannia			-	-	=	=	=	=	=	=	-	-
S. ptychoides	=	=	=	=	=	=	=	=	=	=	=	=
S. filamentosa	-	-	-	-	=	=	=	=	=	=	=	-

In stressed habitats (reef base, coastal mudflats), species diversity of seagrasses and associated macroalgae was much lower than in the other habitats. This low diversity is probably caused by high sedimentation rates, physical instability of the substratum, and lower light levels in the sandy reef base habitat (usually at depths > 10 m). In terrigenous coastal habitats it is probably related to reduced light levels, high nutrient loads and considerable fluctuations in salinity due to river discharges (seasonal effects). Some species (the seagrass *Enhalus acoroides* and the macroalga *Gracilaria salicornia*) showed a different morphology in the coastal habitat in comparison to reef habitats. The size of leaves of *Emhalus acoroides* was considerably larger in the terrigenous coastal habitats than in the reef habitats, which can be regarded as an adaptation to a low light- and high nutrient environment (Nienhuis et al., 1989). The segments of *Gracilaria salicornia* were considerably longer in the terrigenous, coastal habitats than in reef habitats (Figs. 2 & 3), a change which can also be regarded as an adaptation to these environmental differences.

The biomass of the macroalgal component in the seagrass beds was usually low (1.4 to 3.6 g AFDW m^{-2}) (Nienhuis et al., 1989; Erftemeijer, in press) contributing approximately 5–10% to the total above-ground biomass of the seagrass beds in reef flat environments. In stressed habitats (coastal areas near a river mouth and sandy reef bases), however, this macroalgal contribution sometimes reached up to an estimated 50% of the total biomass. Here, the algae showed periods of occasional blooming (e.g. *Enteromorpha* sp., *Gracilaria* spp., *Ulva reticulata*, *Spyridia filamentosa* and *Caulerpa racemosa* at coastal mudflats; e.g. *Chaetomorpha crassa* in reef base seagrass beds) during which biomass reached up to 740 g AFDW m^{-2} (coastal site). Several other dominant species of macroalgae associated with the seagrass meadows also showed a seasonal pattern in their occurrence (Table 5), but never reached a large biomass. The seasonal quantitative importance of macroalgae in seagrass beds in Papua New Guinea was found to be a reflection of substratum conditions, rather than of the presence of a particular seagrass species (Heijs, 1985).

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